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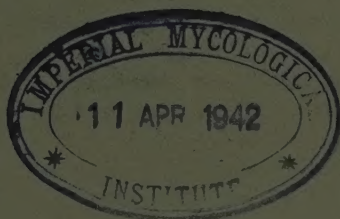
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THE CYTOLOGY OF HOST-PARASITE RELATIONS

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I plan to discuss this topic with special reference to rust fungi. Their host relations, however, can best be appreciated against a background of those of other types of fungous parasites.

The literature covers both mycological and pathological points of view concerning fungous parasites and it is no easy problem to organize this accumulating material with respect to the physiology of parasitism. The latter is by no means a new viewpoint. It was called to the attention of mycologists by de Bary (13) who distinguished: (1) pure saprophytes, illustrated by the type of *Pilobolus anomalus*; (2) facultative parasites, illustrated by *Sclerotinia sclerotiorum*; (3) facultative saprophytes, and (4) obligate parasites, of which the Ustilagineae and the Uredineae are respective examples. In his discussion of these divisions de Bary's emphasis is upon nutrition; he sees a direct causal connection between these grades of parasitism and the process and method of feeding on the part of the fungus.

Bacteriologists, on the other hand, have emphasized invasive power. Bail (11) derives parasites from saprophytes which can under no condition colonize within foreign organisms. The tetanus bacillus is a "necroparasite" with such limited infective power that it can colonize in living organisms only through dead tissue. The infective power of "half parasites" such as the typhus organism can be easily influenced. "Pure parasites," with such high infective power that from a minimum number at entrance the spread through an organism is rapid, are illustrated by the bacilli of hemorrhagic septicemia. Theobald Smith (62) conceives a series of bacterial parasites where offensive devices of invasion give place to such a balance with one host as to allow the parasite to complete a full life cycle of invasion, multiplication and dissemi-

nation. The diphtheria bacillus is chiefly offensive; the tubercle bacillus has developed a preponderance of defensive mechanisms; the spirochaete of syphilis has dispensed largely with both offensive and defensive powers and its metabolism produces little reaction on the part of the host. Raines (56) has indicated how these functions of offence and nutrition may interact. With emphasis, as it were, upon Smith's "one host," he writes: "In the group of the fungi the transition from violent and destructive parasitism to parasitism of the symbiotic type is accompanied by a transition from facultative to obligate parasitism as if the physiological corollary of parasitism of the latter type is extreme specialization in food preferences." He illustrates the violent and destructive parasites by *Botrytis* while the seed fungus of *Lolium temulentum* he calls a benign infestation. Thus both specialization of offensive metabolism and adaptation to the living host may fall into place in de Bary's four-part classification.

There are many interesting examples of facultative parasites in the literature. *Bacterium campestre* causes the black rot of cabbage. Meier's (45) description of the effects of its intercellular masses—invagination of cell walls, disappearance of nucleoli, collapse of nuclei and chloroplastids against the cell walls and decrease in the amount of cytoplasm of the cells—proves it a successful instrument of destruction. In contrast to this type, instances of adaptation of bacterial parasites to their hosts are not lacking. Witness the classic figures of Peirce (54) showing intimate intracellular relations for the tubercle bacterium in the root cells of bur clover.

Among hyphal fungi, Pearson (53) traces the shift from saprophyte to parasite in the corn-seedling blight, *Gibberella Saubinetii*. This fungus exists as a saprophyte on crop refuse and enters the living plant only through wounds or weakened tissue. Here it is first intercellular but it may grow through the middle lamella and later invade the cells. The result is a swelling of cell walls and an accumulation of dark-staining matter in the walls resulting in dark brown, sunken lesions on the seedlings, or of rot of the entire seedling. Emmons (26) has made clear by his studies upon *Cicinnobolus Cesatii* de Bary, parasitic in *Erysiphe Cichoracearum* on *Helianthus tuberosus*, that the offensive parasite by its very success may revert to saprophytism. *Cicinnobolus* is primarily a para-

site. The invading hypha passes through the wall of the host and directly into the host protoplasm, apparently without invagination. It quickly kills the host cells, apparently by "enzymatic action rather than by toxins," if this is a real distinction. *Cicinnobolus* then continues to live upon the dead organic material. Emmons concludes: "It is specialized in its choice of host, in its method of invasion, and in the completeness of its utilization of the materials in its host." Interesting variations of the parasitism of a fungus upon a fungus are to be found in the cases of *Piptocephalis*, *Syncephalis* and *Chaetocladium*, parasitic upon other Mucorini. It was to these that Van Tieghem's (67) term "facultative parasites" was first applied but de Bary (13) considers them facultative saprophytes on the ground that "they only attain to their full development in the formation of zygospores when they live as parasites on other Mucorini."

A graded series of offensive invasions, tending finally toward mutualism, has been traced by Walker (68). *Colletotrichum circinans*, he tells us, can establish itself on onion plants only as a saprophyte on dry, outer skins of the bulb. On the dormant bulb it may succeed in an attack upon the succulent scales but only to become a mildly aggressive parasite. Toxins in the host cell, particularly in cells of the red onion, seem to hold the process in check. Possibly because of these *Colletotrichum circinans* is seldom observed as a wound parasite; it succeeds in an infection only because, after penetration of the cuticle, it causes some degeneration of the host protoplasts in advance of further penetration and thus destroys the host toxins. Walker has recently (69) isolated two water-soluble toxic substances from the outer scales of colored onions and thinks they are responsible, in part at least, for the resistance of these onions. Walker describes a more advanced type of parasitism in the case of *Botrytis byssioides*. This fungus enters usually through old tissues at the top of a bulb. Although it, too, is often inhibited by action of host cell "toxins" it does establish itself to the point where its secretions may break down host tissue in advance. Thereafter it develops rapidly upon by-products of host cell decomposition. Its secretions are thus much more potent for destruction than those of *Colletotrichum circinans*. Walker carries his series one step further into the field of adaptive parasitism by means of *Colletotrichum lindemutheanum* described

by Leach (41). In a resistant host, penetration by the fungus brings prompt disintegration of the host protoplasts and the hyphae are incapable of further development; in a susceptible host, in early stages, there is no evidence of detrimental effects upon the host protoplasts. Passage through walls is by a small opening without effect upon the adjacent wall and without effect upon the protoplast within. Only later, but quite suddenly, does there come a shift in the balance when the advancing parasite causes softening of cell walls and disintegration of cell contents. Walker concludes: "Thus in this early stage the parasite appears to maintain a relation suggestive of the higher type so common with the obligate parasites."

Of much the same nature as this series given by Walker is the series which I have traced (58) for varieties of *Botrytis*, an evolution from saprophytism to parasitism with the conclusion that "both in the occasional finer adjustment between invader and host which brings death less quickly as the result of infection, and in tendencies toward specificity in hosts, this example of a facultative parasite suggests something of the manner of life of the haustorial fungus." However, it is only facultative parasitism at best; and *Botrytis* in its host relations in general illustrates what the obligate parasite with haustoria does not do although showing a very high degree of specificity in its choice of hosts.

The morphological expression of the "extreme specialization in food preferences" which Raines has called the physiological corollary of obligate parasitism is, I believe, the haustorium. This intracellular organ of intercellular fungi exhibits great refinements in its method of wall penetration and of feeding. A compilation (58) of reports from the literature shows that all the great groups of hyphal fungi, Oömycetes, Zygomycetes, Ascomycetes and Basidiomycetes, contain species which produce haustoria. In predominately saprophytic Zygomycetes, haustoria are reported only for one small division; in the other three groups there are subdivisions in each of which their occurrence is practically universal. Mention from these three groups of the Peronosporaceae, the Erysiphaceae and the Uredinales, respectively, as examples of haustorial groups of highly adapted parasites, is evidence that the existence of haustoria may be considered an index of the grade of specialization in the relation of host and parasite.

The feeding function of the haustorium is indicated in such quotations as the following. Latham (40) says of a *Cercospora* leaf-spot fungus of *Vigna sinensis*: "The fungus absorbs at least a part of its nutriment from the surrounding cells by means of haustoria." Weston (71) describes for *Sclerospora graminicola* on Everglade millet, in addition to slender hyphae of transmission: "knotted, much-branched, contorted, feeding hyphae which are crowded into the interstices between cells of the mesophyll and furnished with short, knob-shaped or finger-shaped haustoria." Pady (51) writes of *Hyalopsora aspidiotus*: "the haustorium is essentially a nutritive organ, making possible the growth of the organism."

With the general acceptance of the haustorium as a feeding organ, elaboration of form in the haustorium is, I believe (58), to be regarded as another evidence of a high degree of adaptation by the haustorial parasite in securing maximum contact relations with the host protoplasm. From the small button-like type of *Cystopus candidus*, the species in which haustoria were first described by de Bary (12), the literature reports endless variation of elongation, branching and coiling, culminating in such climax achievements of increased surface as the digitately-branched structures of *Erysiphe graminis* described by Smith (60) or the coral-loid structures in the Asterineae so frequently figured by Arnaud (7). A recapitulation of this development may often be seen within the life time of one species; young haustoria of *Puccinia Sorghi* are slender-stalked buttons but lobing commences early and the mature form is a digitately-lobed structure (58). It follows naturally that such highly specialized structures should have significance as specific characters. Faull (28) states with reference to the haustoria of the Pucciniastreae: "It is worth recording that they are more or less characteristic for each genus." Graff (30) uses the haustorium as the criterion by which to distinguish three grades of parasitism in the genus *Meliola*. In *Meliola circinans* Earle there is no evidence of the presence of haustoria but the superficial mycelium in some way corrodes the epidermal cell walls and causes some injury to the host; in most species, haustoria of a simple type penetrate the epidermal cells; there are also occasional species with haustoria which penetrate to the mesophyll

region. Such forms should be further studied as to their relative effectiveness in their host relations.

There are many instances from the various groups of haustorial fungi where adjustment between haustorium and host protoplast is far from effecting mutualism. Such instances may serve to show steps in adaptation to the living host. Aronescu (8), noting in *Diplocarpon Rosae* the browning of cells penetrated by haustoria, the limited surface of the haustoria and their occurrence chiefly in epidermal cells of rose leaves, says that *Diplocarpon Rosae* seems to be a transition form which has left the lowest step of parasitism but is still far from the level of a strictly obligate parasite. A *Cercospora* upon *Vigna sinensis*, according to Latham (40), causes irregular necrotic areas upon the leaves. The fungus develops rather slowly at first as an intercellular mycelium with haustoria; later, when the attacked cells have reached the necrotic condition, both inter- and intracellular mycelium may be found in the same lesion. Wolf (73) reports that *Peronospora hyoscyami* de Bary develops an intercellular mycelium in leaves of tobacco seedlings from which branched haustoria penetrate the cell walls. After spore production, not only do the invaded cells die but the collapse may involve the entire leaf or the entire plant. As a result of culture experiments, Wolf concludes that toxic water-soluble substances are formed within the diseased tissues and that they may permeate the entire plant.

On the other hand, among that group of facultative saprophytes, the Ustilagineae, where intracellular hyphae abound and haustoria apparently are not a constant feature, there are, nevertheless, striking instances of close adjustment between host and parasite. Butler's observations (17) upon the Ustilagos indicate much variability in the matter of haustoria. Butler reports for *Ustilago Tritici*: "growth is exclusively intercellular; there are no haustoria; and the host cells are not affected in the slightest degree by the presence of the parasite." For *Ustilago Avenae* he reports: "Except at the moment of entry, the hyphae never penetrate into the cell cavities, though they may send in haustoria." For *Ustilago Zeae* he describes "infection hyphae," either inter- or intracellular, and "feeding hyphae" which form little clumps with many branches within individual cells, comparable to haustoria of parasites that live mainly between the cells. Kolk (38) does not men-

tion haustoria for *Ustilago Avenae* in *Avena sativa* var. *Victor* (S. N. 126). She describes both inter- and intracellular hyphae and reports: "compatibility between host and pathogen reaches such a high degree of development that the fungus causes no change in the appearance of the cells, . . . and there is little difference between cells invaded by hyphae and those not." She notes, indeed, a possible stimulation of the host cell to produce more cytoplasm as the hyphae make their way through the host cytoplasm and are surrounded by it to a greater or less extent. Lutman (42) uses the rare occurrence of haustoria in *Ustilago* as a generic character over against that of well developed haustoria in *Tilletia*. He relates this difference to a physiological one, pointing out that the *Ustilagos* live generally in places favorable for food collection, namely, growing points, stamens and ovaries; while the *Tilletias* are more generally leaf or stem parasites and may find these tissues less favorable for a concentrated food supply. It would be of interest to classify the species of the Uredineae upon the same basis. Has the typical and frequent haustorium been so abundantly developed in this group because the species of the Uredineae are characteristically leaf and stem parasites?

A report by Pady (52) describing the occurrence of intracellular hyphae in the orange-rust of *Rubus occidentalis* is of special interest in this connection. Pady made inoculations with a short-cycled strain of *Gymnoconia interstitialis* upon young shoots of *Rubus* and followed the course of infection from the time of inoculation to the appearance of rusted leaves the following year. The germinating basidiospore forms the usual penetration hypha in an epidermal cell but then, instead of developing intercellular branches at once, this penetration hypha develops within the host cell into a several-celled, coiled hypha. From its first, and later from its second basal cell, branches arise which penetrate adjacent cells. Each penetrating branch becomes in turn a coiled hypha from whose base other cells are infected until, by this regularly repeating unit, a hyphal complex is formed which involves many cells. Epidermal and cortical cells are thus invaded but when the phloem is reached the hyphae enter the middle lamella and continue as intercellular runners which send haustoria into the cells. By means of these runners the fungus reaches the root where it

overwinters and the following spring stimulates excessive growth of canes to form a witches broom. The change to intercellular runners begins about twelve days after inoculation; the intracellular hyphae appear to act for a time in haustorial capacity but their formation slows down as the intercellular mycelium becomes well established with haustoria; they are not found in the second season's growth. Pady thinks that this intracellular device is a temporary stage in the establishment of the systemic infection. It is important to this establishment that the mycelium reach the phloem as rapidly as possible if it is to reach the roots before the end of the growing season. Intracellular hyphae by making rapid feeding contacts could further this end. This interpretation of Pady's might apply to the Ustilagos. Perhaps with these smuts the presence of intracellular hyphae instead of haustoria relates to a need of rapid growth from places of infection in seedlings to places of sporulation in growing points, stamens and ovaries. Pady's interpretation indicates the haustorium as the organ of restrained feeding by the mature parasite. Lutman, suggesting that haustoria are not developed in regions of easy feeding, indicates the haustorium as an organ developed to overcome difficult conditions. Pady's work reopens the question. It may be noted that the haustorial parasite *Cercospora* upon *Vigna sinensis* (40) was said to cause little effect upon the host in its early haustorial stage but later when the attacked cells had reached the necrotic stage both inter- and intracellular mycelium was found.

Among the Uredineae lack of disturbance of the host cell by the parasite is the usual effect although occasional exceptions have been reported. Dodge (20) reports an exception in red cedar infected by *Gymnosporangium germinale*. Here the cells bordering upon hyphae, especially cells invaded by haustoria, soon show much disorganization. A nice contrast may be seen between the non-disturbing effect of the haustorium and the host cell death caused by development of intracellular spores in Pady's (50) description of teliospore development in *Calyptospora goeppertiana* in stems of *Vaccinium pennsylvanicum* and *Vaccinium canadense*. The contrast cannot be seen in Pady's figures of haustoria and teliospores in the host cells since he does not figure host cell cytoplasm or nucleus. In his text, however, he describes an early stage of infection where there are abundant haustoria in the cortical cells

and he writes of the external appearance of the stems at this stage: "The young infected shoots may readily be distinguished from normal shoots by their slightly larger size, pale green color and soft, fleshy appearance." For the later stage in which the cells contain spore initials as well as haustoria we read: "the contents of the epidermal cells begin to disintegrate and the pale green color of the stem disappears." Still later, the thick-walled teliospores in the epidermal cells give the stems a varnished, dark-brown appearance.

Not only do rust parasites cause a minimum of disturbance in the host cell but many instances have been reported of actual stimulation of the host protoplast. The gross phenomena of witches brooms in *Juniperus virginiana* infected by *Gymnosporangium nidus-avis* (66) and the huge galls of *Pinus rigida* infected by *Peridermium cerebrum* Peck (21) are familiar illustrations of hypertrophy and hyperplasy induced by rusts. The distortions produced upon *Rivina octandra* by *Puccinia Rivinae* (10) are an extreme manifestation of stimulation by the aecidial stage of a rust. However, in all such structures the infected host cells are the units where the interrelation between host and parasite needs to be observed. One is impressed by the evidence that at least for all early stages galls are the result of "the integrating activity of the cells themselves (31) rather than a disease abnormality." The galls on leaf and stem of *Sambucus canadensis* infected by *Aecidium Sambuci* are favorable for such study (58). A section shows that the enlarged mesophyll cells are surrounded by intercellular hyphae from which one or more haustoria enter nearly every cell. There is no plasmolysis and the nuclei of the host cells show phases of mitosis undergone while in contact with haustoria. Dodge (20) has made a cytological study of *Gymnosporangium myricatum*, perennial in *Chamaecyparis thyoides*, and finds there a rejuvenation of fairly old and collapsed cortical cells whenever hyphae of the advancing mycelium come near them. By this stimulation parenchyma strands burrow into the cortex like a cancerous growth.

In the matter of wall penetration the habit of the haustorium is foreshadowed even among some of the facultative parasites where the normal habit is an offensive metabolism such as Orton (48) describes for *Phyllachora graminis* upon *Agropyron repens* and

Catacauma flabellum upon *Pteris aquilina*. "Both are conspicuous," he writes, "for their ability to penetrate the cell walls of their hosts by dissolution." In contrast to this habit Brown and Harvey (16), after observations upon *Botrytis cinerea*, conclude that its means of penetration is purely mechanical. Abdel-Salam (2) supports this view, reporting for *Rhizoctonia Solani*, *Rhizoctonia violacea* and *Pythium* sp. upon lettuce that all these penetrate the cuticle by thin, peg-like, hyphal outgrowths which bore their way through the wall and then resume their normal thickness. This latter is the accepted method for obligate parasites. It is the habit of an haustorium to penetrate the host wall by means of a slender filament without any digestive action. Bolley (14) states of the rusts: "(they) are such perfect parasites that the hyphae pass directly through living cell walls of the host and make practically perfect fusions with the cell walls."

More distinctive even than this refinement in wall penetration by the haustorium is the lack of any puncturing or actual penetration of the primordial utricle of the host cell. Invagination of the primordial utricle which results in an increase of absorbing surface for the fungus without actual invasion of the protoplast is a generally accepted character for the haustorium. Arthur (9) states: "It is probable that in no instance does the haustorium come into organic contact with the protoplasm of the host-cell." The importance of this habit as an adaptive character lies not merely in the fact that there is no actual penetration of the host protoplast, but in the lack of disturbance of the protoplast which invagination implies. Such occasional exceptions as Dufrenoy's (23) report of plasmolysis by haustoria of *Uromyces Caladii* in *Arisaema triphyl- lum* may, I think, be due to confusion between intercellular hyphae and haustoria (59). Dodge (19) has also called attention in the case of *Diplocarpon Rosae* to the possibility of confusion between inter- and intracellular hyphae.

Dufrenoy (25) has made detailed studies of a large number of plant parasites including both facultative and obligate parasites, both mosaic and hyphal forms. He finds in all an identical host effect, that is, death resulting more or less rapidly from increased proteolytic activity. He writes: "Be it physical as evidenced in glandular cells of hairs of carnivorous plants (*Drosera*) or pathological as in cells affected by microscopic parasites or by viruses,

enhanced biochemical activity is evidenced by a division of the bulk of the involved cytoplasm into a number of slender films, spreading and forking into vacuolar material as so many partitions, which divide a large vacuole into a number of smaller ones. When the partitioning off is carried to an extreme the cytoplasm assumes a honey-combed appearance which has been described in virus-affected cells under various names but corresponds to similar structures resulting from local proteolytic activity induced by penetration of fungus haustoria, or that can even be observed in cells of tissues starving under aseptic conditions." This similarity of effect does not fit with my own observations. I agree rather with Aronescu (8) who says: "It seems that different effects and more serious ones must be expected in the cytoplasm of a host cell which has been penetrated by a hypha of a facultative parasite which does not form any haustoria, than the effects produced by a haustorium which has invaginated only the cytoplasm." In so far as my figures suggest an increase in mass of the primordial utricle I regard it as a matter of hydrolysis rather than such formations of "slender films spreading and forking into vacuolar material as so many partitions, which divide a large vacuole into a number of smaller ones."

From considerable study of plant tissues infected by rusts I am convinced that the rust parasites at least have so adjusted their demands to the metabolism of the host that a host cell surrounded by intercellular hyphae and invaded by haustoria looks, nevertheless, strikingly normal and healthy. The series of drawings shown on plate 1 is an attempt to show such conditions. They are drawn from living tissues of six different rusted plants gathered under varied conditions. Five of the six show perennial rusts. The tissues were mounted in 8 per cent sugar solution or in alcohol followed by lactophenol. The mounts were all examined under oil immersion lenses.

Figures 1 and 2 show epidermal cells from leaves of *Arisaema triphyllum*. Several *Arisaema* corms were dug up in October, 1934, washed and planted in fresh soil in the plant house. By December the plants had leaved out. Figure 1 shows a cell from the lower epidermis of a plant infected with *Uromyces Caladii* Farlow. Spermatogonia were in evidence on the leaf as soon as it appeared above the soil in December; they were fully developed

and were exuding a yellow fluid on the green leaf when the lower epidermis was stripped and mounted, inner side up, in 8 per cent sugar solution. The cell drawn lay only two cells distant from a spermogonium. The hypha which produced the haustorium belonged to the intercellular mass which ramified between mesophyll and lower epidermis and lay thus above the epidermal cell. These are conditions of heavy infection yet the host cell appears no more highly vacuolate than does the uninfected epidermal cell of figure 2 and there are no precipitation products in the vacuole.

Figures 3 and 5 are from a carnation leaf picked in February 1935 from green house stock heavily infected with *Uromyces caryophyllinus* Wint. The areas immediately around the erumpent pustules of uredospores were slightly paler than the rest of the leaf but the rusted leaves were firm and the plants were vigorous. The stripped epidermis was mounted in 8 per cent sugar solution, in inverted position. Figure 3 shows a haustorium in an epidermal cell; figure 5 shows two of the overlying mesophyll cells and hyphae which lie between these and the epidermis. The chloroplastids in the mesophyll cells were green and healthy in appearance and the cytoplasm, except where invaginated around the haustoria, was in normal position close to the wall, around the large central vacuole. The slightly different levels of the two haustorium-mother cells result in different views of the penetrating stalks of the two haustoria.

Figure 6 shows an epidermal cell from a leaf of *Potentilla canadensis* infected with *Phragmidium Potentillae-canadensis* Diet. When this perennial rust was gathered on March 16, 1935, the orange sori of uredospores were already swollen under the epidermis of the green, over-wintered leaf. The stripped epidermis was fixed in 95 per cent alcohol and mounted in lactophenol.

Figure 7 shows two parenchyma cells from an over-wintered hollyhock leaf which was fresh and green when picked on March 4, 1935, only two days after the winter snow had melted from the bed. Pustules of teleutospores of *Puccinia Malvacearum* Mont. were abundant over the leaf. The mount was a strip of epidermis in lactophenol following 95 per cent alcohol. The cells drawn lay directly below a pustule on the under surface of a vein. The penetration stalk of the haustorium in the smaller cell is drawn at the level of the intercellular hyphae. The massing of cytoplasm

around this haustorium is possibly a reaction against the parasite but there is no fragmentation of the host cell vacuole and there is the usual evidence of invagination.

Figures 4, 8, and 9 show cells of *Pyrola americana*. Figure 4 shows an epidermal cell from a strip of lower epidermis from a normal, unrusted plant. It was mounted in sugar solution. The epidermal cells of *Pyrola americana* contain chloroplasts; the cytoplasm is, for epidermal cells, unusually abundant and is frequently alveolar in appearance. Figure 9 shows two cells from the under epidermis of a *Pyrola* leaf infected with *Chrysomyxa Pyrolae* Rostr. The epidermis was mounted in sugar solution and stained with 10 per cent neutral red. This perennial rust on *Pyrola* in the spring develops uredo and teleutosori on the overwintered leaves while the new leaves of May show no rust until the following spring. The leaf, when picked on April 7, 1935, showed many uredosori under the unbroken epidermis. The cells figured lay close beside a group of sori and a heavy felt of intercellular hyphae overlay much of the inverted epidermis, projecting from under the adhering mesophyll cells. The chloroplasts in the cells figured were as deep a green as in uninfected cells. The alveolar structure of the cytoplasm in the larger cell is perhaps more noticeable than in the smaller cell of figure 4. The neutral red stain, however, indicates the normal condition of this cytoplasm; it stains the vacuole and not the cytoplasm. This cell certainly does not show the condition described by Dufrenoy (24) who says that in cells infected by rust the vacuole fragments itself in such fashion that the haustorium is surrounded by an aureole of small vacuoles, and further that, while certain vacuoles retain the neutral red stain, those in the neighborhood of a haustorium form vacuolar precipitates. At the plane figured, invagination of the host cell cytoplasm is evident. The heavily sheathed haustoria, when viewed at a higher plane than that figured, were completely veiled in the host cytoplasm, so that they appeared like inflated masses of cytoplasm. It is difficult with this fresh material to draw conclusions as to the nature of the haustorial sheaths or of such basal sockets as that in figure 7. However, in microtome sections of fixed material of *Pyrola* rust (58), the sheath takes the same stain as does the host cell wall. Most haustoria in epidermal cells of *Pyrola* are heavily sheathed and are quite generally

shrunk within the sheath. Figure 8 shows the typical haustorium found in mesophyll cells of a *Pyrola* leaf. This drawing was made from a free-hand cross section of a fresh leaf. The section was mounted in glycerine; plasmolysis in the host cell was due to conditions in the glycerine mount but it does not obscure the evidences of invagination around the haustorium.

Chrysomyxa Pyrolae is the only one of the rusts figured in this article which shows sheaths around the haustoria. An enclosing sheath about haustoria, varying from cup or collar to complete enclosure, is as variable yet distinctive a character for different species as the haustorial form. When it arises in connection with a thickened wall at the point of penetration of an haustorium it appears to be a host cell product. Smith (60) describes such a formation for *Erysiphe graminis*. Tai (65) gives almost the same explanation for the interaction of *Juniperus chinensis* and *Gymnosporangium Yamadae-Miyabe*. The host cell is stimulated by the penetrating haustorium to build a protective sheath but there is a limit to this defensive activity and then the haustorium digests away all but a thin investing membrane. Moss (46) finds in the Pucciniastreae all stages of the sheath from absence to complete enclosure. He gives a generally accepted view in the statement: "It appears that the sheath is laid down by the surrounding protoplasm of the host in response to a stimulatory action of the haustorium. Undoubtedly this constitutes a defense on the part of the host cell because the encapsuled haustoria are in disorganized condition." The sheathed haustoria of *Chrysomyxa Pyrolae* shown in figure 9 are evidently disorganized but according to other observations (58) sheathing does not by any means result always in disorganization. Many haustoria of both *Puccinia Sorghi* Schw. and *Aecidium claytoniatum* Schw. are plump, nucleated structures within heavy sheaths. It would contribute toward an explanation of the significance of the sheath if the development of the mycelium in leaves of *Pyrola* were followed to determine whether the sheathed haustoria in epidermal cells are formed early or late in the spreading infection, whether they are the result of a weakening parasite, of a host especially vigorous at the beginning of leaf infection, or of a host whose epidermal cells are more able than other leaf cells to build sheaths because of their habit of building thick walls. Figures 3

and 9 show the characteristic thick walls of epidermal cells of *Pyrola*. There remains also the unsolved problem of thickenings on the haustorial stalk not in connection with the host cell wall such as I have reported for *Puccinia Sorghi* (58). Here again *Pyrola americana* offers especially favorable material because of the abundant cytoplasm in its cells. In figure 9 the stalk of the haustorium in the smaller cell is seen in external view instead of in section as in the larger cell. Across the stalk may be traced the line of both plasma membrane and tonoplast. Are these structures of the cell especially potent in the laying down of wall substance? The effect of a sheath upon the feeding of the enclosed parasite is also open to debate. The inference seems a safe one which Aronescu (8) makes for *Diplocarpon Rosae* that a sheath reduces the absorbing surface of an haustorium. To this statement I would add: "If cellulose walls allow the passage of food through them into intercellular hyphae, then cellulose sheaths can at best merely lessen the amount absorbed" (58).

The remaining figures on the plate are studies of *Aecidium punctatum* Pers. and its host, *Hepatica acutiloba*. On February 12, 1935, several *Hepatica* plants were lifted from under two feet of snow and brought into the plant-house. On February 16 the winter buds had opened and blossoms had appeared. On one plant leaves instead of blossoms were pushing up. This indicated rust as *Aecidium punctatum* induces sterility in *Hepatica*. The leaf picked for study was only just above the soil and its lobes were closely rolled but the under surface was dotted with spermogonia, each capped with a drop of pale yellow fluid. The epidermis was stripped off and mounted inner side up in 8 per cent sugar solution. Figures 11 and 13, drawn from this tissue, show the dense contents and relatively large nuclei of the cells from this rolled leaf and show the line marking the surface of the invaginated cytoplasm around each stalked and coiled haustorium. Figure 10 shows a cell from the lower epidermis of an older leaf from the same plant. This leaf was cut on February 20 after it had expanded into the stiff, long-petioled blade which is characteristic of rusted *Hepatica*. The spermogonial liquid had deepened to orange-yellow and aecidia showed as white spots beneath the epidermis. The epidermis was mounted in 8 per cent sugar solution. The figure shows a larger host cell vacuole and a more elaborately

coiled haustorium than those in the younger leaf. Both of the infected *Hepatica* leaves were thickly studded with spermogonia and practically the whole leaf area between lower epidermis and mesophyll was crowded with intercellular hyphae from which haustoria entered the cells above and below. Figure 10 shows an overlying hypha from which a haustorium arises; figure 13 shows in cross section an overlying hypha from which a haustorium enters one of the cells. Figure 12 shows cells from the lower epidermis of a leaf of an unrusted plant. This leaf, following the regular habit in *Hepatica*, developed after the plant had finished blooming but it was, when picked, in the same closely rolled stage as the one from which figures 11 and 13 were drawn. A comparison of figure 12 with figures 11 and 13 proves that the infected host cells are close to normal in appearance. The cells of the infected leaf show the same conditions of nuclei, cytoplasm and vacuoles as those of the uninfected leaf of the same age. Variations in these cell structures are evidently physiological and not pathological effects.

Only second to the question of invagination, in any discussion of haustorial host cell relations, is the question of the reaction of the host nucleus. I am repeatedly impressed with the very normal spherical shape and normal size of the host nucleus in the majority of infected cells. In a set of forty-three drawings of cells from corn tissue (58), of varying age and varying degrees of infection with *Puccinia Sorghi*, twenty-three of the cells showed nuclei; only four of these nuclei were abnormally large; only two of these were lobed. I have found more striking instances of enlarged, lobed nuclei in galls upon *Sambucus canadensis* infected with *Aecidium Sambuci* Schw. and in leaves of *Claytonia virginiana* erumpent with spermogonia and aecidia of *Aecidium claytoniatum* Schw. That these abnormal shapes do not of themselves predicate ill health has been pointed out by Goldstein (29) who finds that hypertrophied, irregularly lobed nuclei occur normally in healthy plants, in special organs of nutrition, and associated with certain phases of nutritional and secretory activity.

Contact between haustorium and host nucleus seems, both from reports in the literature and from my own observation, to be a variable phenomenon but a large majority of investigators report that haustorium and host nucleus are habitually or frequently in

contact. Cunningham (18) goes farther than this stating for the rusts: "when entry is effected the haustoria invariably grow in the direction of the host nucleus." Dodge (19), reporting upon *Diplocarpon Rosae*, indicates the opposite view in the statement: "No evidence has been found to indicate any particular attraction or repulsion as to the relation of haustorium and host nucleus." As to which member brings about the contact and for what purpose there is little unanimity in the reports. They include purposes of defense and offense by the nucleus and a furtherance of absorption by the haustorium. The latter purpose seems to fit the specially adapted haustorium but it presupposes active growing of the haustorium toward a movable part of the protoplast. Allen (6) makes a case against this in her observations of *Puccinia glumarum* on *Bromus marginata* and *Triticum vulgare* since in the 82 per cent of contacts reported in her observations of this rust many of the haustoria were located at the end of a cell three or four times as long as the haustorium. The contact between the two can have been achieved, she thinks, only by the motion of the nucleus toward the haustorium.

Probably the most delicate indicator of health in a photosynthetic plant is the chlorophyll. Hence, by this indicator one can most effectively recognize the delicate adjustment of the haustorial parasite to the host cell over against the devastating action of the non-haustorial facultative parasite. Two instances of this devastating action follow: a fungus upon *Zostera marina* thought by Peterson (55) to be *Ophiobolus maritima* blackens the infected cells and causes finally the death of the leaf; *Fusicladium saliciper-dum* (15) blackens infected cells of willow leaves in ever widening zones until the whole leaf may be affected. Brooks and Walker are undecided whether this death of cells beyond the infected zone is due to products which diffuse from the cells first killed or to toxic secretions of the fungus itself. Mosaic diseases illustrate a less destructive effect but Nelson (47) states: "Chloroplast degeneration seems to be one of the microscopic symptoms of mosaic disease in many plants." Even many of the haustorial fungi show disturbing effects upon chloroplasts. Weston (71) states that the systemic infection of *Sclerospora graminicola* on Everglade millet shows itself chiefly in the development of pallid, yellowish markings in the dark green tissue of the leaf. R. E.

Smith (61) reports disorganization of the chloroplast in cells of asparagus when entered by haustoria of *Puccinia Asparagi*. He thinks the immediate collapse and clumping of the chloroplasts is due to some soluble substance, poisonous or enzymatic, excreted by the haustoria. The hosts of aecidial infections are frequently chlorotic. For example, plants of *Houstonia coerulea* infected with *Aecidium houstoniatum* are markedly etiolated (58). Dufrenoy (22) states that galls formed on chlorophyll tissue if not colored by anthocyanin are usually colorless. He reports galls upon leaves of *Asphodelus subalpinus* infected by *Puccinia Asphodeli* in which there is an exaggerated activity of chlorophyll concomitant with the growth of the young galls but a discoloration of adult galls concomitant with the development of enormous tannin vacuoles and an accumulation of reserve starch. In still another case of an aecidial infection Reed and Craybill (57) report that the palisade cells in the rust lesions of *Gymnosporangium Juniperi-virginianae* contain carotin and erythrophyll but no chlorophyll. I can endorse reports of the yellowing effects of this rust. A pasture grown up to thorn apple trees drew my attention one July because practically all the leaves were spotted with orange. The orange coincided with thickened leaf areas which bore the roestelia of *Gymnosporangium Juniperi-virginianae* Schw. Cytological examination of the leaves showed that the space between the upper and lower epidermis of the infected areas was packed with enlarged cells making a cushion four times the width of the uninfected, green portions of the leaves. The cells of the infected area were abnormal only in size. Their chloroplasts, instead of being disintegrated as the yellow color might lead one to expect, were larger than those in the green areas beyond the infection and were swollen with grains of assimilation starch. Apparently the photosynthate was drawn from its place of manufacture to the infected cells. Such a drain must eventually lead to disorganization even with a highly adapted parasite. Any observer of rusts knows the starvation and dessication effects which attend sporulation in heavy rust infections of the cereals. Cunningham (18) states: "The annual losses to agriculture caused by 'Rusts' have been computed at upwards of £100,000,000 sterling in cereal crops alone."

In contrast to the above effects, Lamb (39) writes of *Puccinia Prostii* infecting *Tulipa sylvestris* var. *odorata* that the pustules

cause no discoloration of the surrounding leaf tissue. The many examples from the Uredineae of effects similar to that of *Puccinia Prostii* seem to warrant treating the Uredineae as the climax type in the above series. For the rusts which I have shown in plate 1 there is no need to qualify the statement that there is no discoloration around the pustules. The winter rosettes of *Potentilla canadensis* on the lawn catch one's eye because of the orange pustules on the green leaves. The green surfaces of *Pyrola* leaves in the spring woods make a striking contrast to their orange under surfaces where uredo pustules have destroyed the epidermis. These leaves wither as the new leaves develop but apparently not much sooner than those of uninfected plants. The spring leaves of *Hepatica*, metamorphosed into stiff, long-petioled blades by the rust, are green even when their under surfaces are covered by the flower-like aecidial cups. These infected leaves, however, wither by mid-summer and are replaced by a cluster which develops without any sign of rust and persists over the next winter as do the leaves of uninfected plants. *Chrysomyxa Pyrolae* and *Aecidium punctatum* are both outstanding examples of restraint on the part of the parasite toward the hosts in which they perennate but with the difference that *Chrysomyxa Pyrolae* comes to fruition on the over-wintered leaves while *Aecidium punctatum* fruits on the new spring leaves.

More striking even than the lack of discoloration in rust-infected leaves is the intensification in color and the lengthened life of chloroplasts found in many rust infections. "The basic fact here is (58) of course the prolongation of the life of the entire cell, and not merely the persistence of the green color." This so-called "green island" phenomenon is a decisive illustration of a longer life given to infected cells under conditions of adversity to the host plant. From this standpoint both "green islands" and gall formations are stimulation effects which differ only in degree. Wingard (72), illustrating bean strains resistant to *Uromyces appendiculatus*, shows an island of green tissue in the discolored flecks due to abortive uredosori. Here the cells in the center of the infection seem stimulated to more vigorous conditions than the cells at the border of the flecks which are in the early stages of invasion by the rust. A study of leaves (58) made in September from a field of Golden Bantam corn infected with *Puccinia Sorghi*

shows "green islands" on the lower leaves. Here the condition of adversity was the drying incident to the normal dying of the older leaves at this late season. Green-bordered sori are figured abundantly in a yellowing but still succulent leaf; they are present in a nearly dry leaf; and a few persist in a dry, brown, basal leaf. Mains (43) explains this phenomenon as due to a levy made by the infected cells upon the uninfected cells surrounding them. Thus the cells of the infected area are supplied with water and are kept in fair health long after the uninfected cells have dried up.

A comparison of this phenomenon with that of the "shot-hole" effect indicates again the higher adaptation of the Uredineae. In the rust infection there is little or no defense reaction by cells surrounding an infection whereas Higgins (32) explains the "shot-holes" in *Prunus virginiana* infected by the haustorial fungus *Cylindrosporium* as due to a defense action set up by cells bordering the infected spot. These become an abscission circle of heavy-walled cells which cut off water from the "spot." Then the infected cells shrivel and drop out.

The same contrast between the poorly and the highly adjusted host-parasite complex may be seen with the one rust in a resistant and in a susceptible host. Allen (4) draws a picture "of excellent congeniality" for *Puccinia triticina* physiologic form 11 on Little Club wheat. "The fungus," she says, "attains its maximum development. . . . The host tissues live, their cell walls (except in the guard cells at the stoma of entry) are not damaged, and the cell contents show a minimum of disturbance or impoverishment." Her description of the same rust form on the resistant Malakoff wheat (5) corresponds to the effects of an offensive, facultative parasite. The first host cells invaded collapse and die promptly. Many of the rust fungi die also; as the survivors succeed in entering host cells and forming haustoria the host reaction becomes milder and a few of the mycelia may bear small uredinia. There is as with *Cylindrosporium* a change beyond the fungus—cells bordering the infected area show irregular, swollen walls.

In this description of the reactions observed in a resistant host one notes emphasis upon the haustorium as the organ which effects a fine adjustment between host and parasite. Hull also (34), discussing types of resistance to *Puccinia Sorghi* shown by *Zea Mays*, says that if the growth of the invader in a resistant host is

rapid enough to make haustorial contacts with host cells before the latter have time to establish any antagonistic response there is then a perfect equilibrium between host and fungus and henceforth formation of haustoria produces no noticeable reaction in the host cells. Such descriptions indicate "the host cell as the place where resistance is expressed, and the attempted penetration of a haustorium as the act by which resistance is stimulated" (58).

The literature offers in increasing number theories concerning the nature of plant resistance to fungus parasites. Wingard (72) concluded a study of rust-resistant beans as follows: "Rust resistance in beans can best be explained on the basis of the hypersensitiveness of the host to the parasite. The immediate destruction of the host tissue results in the death of the parasite because the rust fungus is an obligate parasite and cannot survive in dead tissue." In this sense resistance arises from lack of adjustment. The fungus corresponds to a facultative parasite except that it cannot live upon dead tissue. Allen's description, already quoted, of rust in resistant Malakoff wheat is an illustration (5). Allen states also (3) that immunity is due to definite antagonistic chemical interactions between host and parasite. Stakman early concluded (63) that the problem as to the instruments of immunity called for biochemical investigations. Ezekiel (27) has carried out such an investigation by testing the growth of urediniospores in hanging-drops of materials extracted from normal as well as infected wheat tissues. He found that the extracts affected the growth of physiologic forms of *Puccinia graminis tritici* in a manner diagnostic of the resistance of the host to the various physiologic forms. He concluded: "These materials in the plant tissues presumably explain the phenomenon of physiologic resistance to stem rust." In one experiment Ezekiel found that differentiation was greater with extracts from inoculated plants than in extracts from normal plants and suggests that antibody activity may be, but is not necessarily, involved. This suggestion points out a problem on which much work needs to be done. I think it likely that we are too apt to explain a lack of adjustment between fungus and host as due to toxins. It is possible that the answer to the problem as to the instruments of immunity to an adaptive parasite lies neither in toxins nor in antibodies but, as Mains (44) has suggested, in the normal metabolism of the various hosts. Con-

versely then susceptibility would be brought about by a fungus whose metabolism has been closely adjusted to and linked with the metabolism of a host. Wellensiek (70) really subscribes to this theory when he writes that in corn "resistance to *Puccinia Sorghi* is the expression of starvation of the parasite."

It is the very fact of obligateness, that is, of a high degree of specialization in hosts, which has furthered the breeding of rust-resistant plants. Aamodt (1) points out: "Narrow specialization of the parasite with definite host reactions for the different forms has made it possible to analyze the pathogene and to study its host relationships in such a way as to be of considerable assistance to the plant breeder." He contrasts this condition with the greater difficulty met with in breeding varieties resistant to the foot-rot organisms such as *Ophiobolus*, *Helminthosporium*, and *Fusarium* because of the lack of definite and characteristic reactions of the hosts to the different pathogenes and their physiologic forms, and to the wide parasitic range of physiologic forms in their ability to attack different varieties. The rusts, of course, are not alone in this class of physiologic specialists but that they are eminent members of the class the familiar history of *Puccinia graminis* proves. Stakman wrote in 1926 (64): "*Puccinia graminis* long ago ceased to be merely *Puccinia graminis*; it first became *Puccinia graminis tritici*, *Puccinia graminis secalis*, etc. Now it has even become *Puccinia graminis tritici*, physiologic forms 1 to about 50, inclusive." The list has grown. In February, 1935, Humphrey (35) reports: "Over a hundred distinct parasitic strains or physiologic forms of the stem rust of wheat have been discovered, more than 50 of which occur in the United States." To date he adds (36): "a few additional physiologic forms have been included in the list, bringing the total number up to something like 152, not all of which occur in the United States." Such a record supports Orton's statement (49): "all the evidence available at the present time appears to point to the conclusion that within the Uredinales the trend is toward increased physiological specialization." This record for *Puccinia graminis tritici* is, of course, the result of intensive work carried on largely because *Puccinia graminis tritici* is an enemy to agriculture. It at least indicates what a rust can do when its host is a plant which offers many varieties. This raises another side to the problem of specialization. Jackson (37) writes: "To a

close student of the rusts it is evident that the host has been a very important factor in the evolution of species in this group. As the higher plants have gradually developed during past ages, the rusts parasitic upon them have likewise undergone development."

One returns from a consideration of the rusts to de Bary's classification of fungi with a fuller understanding of the term obligate parasite. The condition for the rusts is summarized by Hotson (33) as follows: "The Uredinales include a group of very highly specialized fungi which are obligate parasites. As far as is at present known they can grow only on living plants (the hosts) and when these are killed the rust dies. Many rusts are so highly specialized that they confine their activities to relatively few species of the host, some to a single species, others to different species in the same genus; rarely do they produce the same spore-forms on more than one host family." We have found that specialization is a corollary to obligateness; the high degree of specialization has been effected, I believe, by the elaborate development of the haustorium. The result is a condition which de Bary (13) places close to that of the lichens on the basis of the limited host accommodation on the part of both rusts and lichen fungi. While the mutualistic nutrition of the lichens is, of course, not paralleled in the rusts the habits of the majority of rusts indicate a restraint in feeding and a reduced or entire absence of toxic action upon the host by the parasite. In the case of "green islands" one might perhaps call the relation between the rust and the host cells temporary mutualism.

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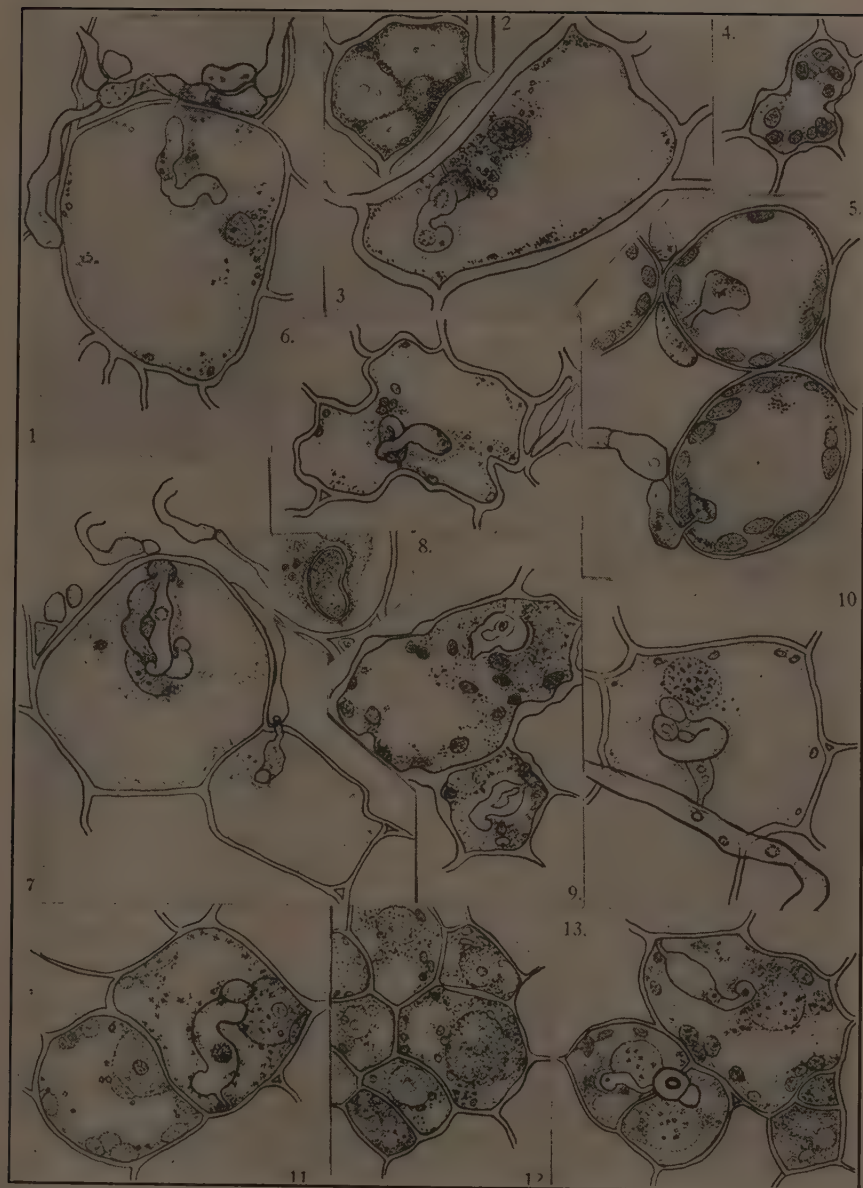
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DESCRIPTION OF PLATE

The figures of Plate I were drawn with the aid of a camera lucida from free-hand sections of fresh leaves. A Spencer microscope was used with an apochromatic objective, 4 mm., and ocular, 10 X, giving an approximate magnification of 650 for the outlines. For details of the drawings a 1/12 inch oil immersion objective and an ocular 10 X were used.

PLATE I

- Fig. 1. Cells from lower epidermis of a leaf of *Arisaema triphyllum* infected with *Uromyces Caladii* Wint., showing intercellular hyphae and a haustorium. Mounted in 8% sugar solution and stained with 10% neutral red.
- Fig. 2. Cell from lower epidermis of a leaf from an uninfected plant of *Arisaema triphyllum*. Mounted in 8% sugar solution and stained with 10% neutral red.
- Fig. 3. Epidermal cell from a leaf of *Dianthus caryophyllus* infected with *Uromyces caryophyllinus* Wint. Mounted in 8% sugar solution.
- Fig. 4. Cell from the lower epidermis of a leaf of an uninfected plant of *Pyrola americana*. Mounted in 8% sugar solution.
- Fig. 5. Mesophyll cells adhering to the strip of epidermis used for figure 3, showing haustoria and the hyphae which lie between epidermis and mesophyll. Mounted in 8% sugar solution.
- Fig. 6. Cell from lower epidermis of leaf of *Potentilla canadensis* infected with *Phragmidium Potentillae-canadensis* Diet., showing a haustorium. Fixed in 95% alcohol and mounted in lactophenol.
- Fig. 7. Parenchyma cells of a hollyhock leaf infected with *Puccinia Malvacearum* Mont., showing haustoria and intercellular hyphae. Fixed in 95% alcohol and mounted in lactophenol.
- Fig. 8. Detail of mesophyll cell from leaf of *Pyrola americana* infected with *Chrysomyxa Pyrolae* Rostr., showing haustorium. Mounted in glycerine which caused plasmolysis.
- Fig. 9. Cells from lower epidermis of leaf of *Pyrola americana* infected with *Chrysomyxa Pyrolae* Rostr., showing sheathed haustoria within invaginated cytoplasm. Mounted in 8% sugar solution.
- Fig. 10. Cell from lower epidermis of a half grown leaf of *Hepatica acutiloba* infected with *Aecidium punctatum* Pers. A coiled haustorium arises from an intercellular hypha which lies above the cell. Mounted in 8% sugar solution.
- Fig. 11. Cells from the lower epidermis of a young, rolled leaf of *Hepatica* infected with *Aecidium punctatum* Pers., showing a haustorium. Mounted in 8% sugar solution.
- Fig. 12. Cells from the lower epidermis of an uninfected leaf of *Hepatica acutiloba* at the same stage as the leaf of figure 11. Mounted in 8% sugar solution and stained with 10% neutral red.
- Fig. 13. Cells from the lower epidermis of the same leaf as that of figure 11, showing haustoria and cross sections of intercellular hyphae. Mounted in 8% sugar solution.



LIGHT¹ AS AN ECOLOGICAL FACTOR AND ITS MEASUREMENT

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Light is one of the most important factors in the growth of plants and also one of the most difficult to study. In order to understand many of its specific effects, workers have resorted to experiments in small chambers using artificial light, and in so far as possible, artificial climate also.² Such experiments are invaluable for discovering the fundamental influences of light and form the basis upon which ecological data can be interpreted.

During the past 15 years, another method of studying the light relations of plants has been widely used. This consists of measuring the daily course of photosynthesis of plants growing in natural habitats and in correlating the photosynthetic rate with light, carbon dioxide supply, stomatal aperture, temperature and other factors. These studies, together with those on the rate of growth of plants in various habitats, are leading us more and more toward an understanding of the reaction of plants to their environment.

The variations in light conditions to which plants are subjected, may be grouped into two classes:

1. Those variations which are caused by differences in latitude, altitude and climate.
2. Those variations which are caused by local obstructions such as forest canopies.

Both classes of variation include differences in the intensity and quality of the light.

Light-Climate

The term "light-climate" (*Lichtklima*) was introduced by German workers (132) to designate the light conditions prevailing in

¹ The term "light" will be used in this paper as synonymous with solar radiation received at the surface of the earth unless otherwise qualified.

² In the Division of Biology and Agriculture of the National Research Council, a subcommittee on Survey of the Committee on Radiation is preparing, with the collaboration of a large number of individual workers, a comprehensive report on the influence of radiation on living organisms which will also include methods of measuring radiation. In this paper the writer is limiting the treatment mainly to the ecological phases which will not be included in the above mentioned report.

various habitats. The writer prefers to restrict the use of this term to the variation of class 1; however, the same term may be used for both by designating class 1 "Macro-light-climate" and class 2 "Micro-light-climate."

The intensity and quality of light received at any point on the earth's surface depends upon the solar constant,³ the distance of the sun from the earth, and the absorption and diffusion of light by the atmosphere. From the standpoint of the plant ecologist and plant geographer, variations in the solar constant are insignificant. However, it is important to know the maximum intensities of light which may be received at the earth's surface, and how these compare with the values reported by investigators in ecology and physiology: The highest values of solar radiation ever measured at the surface of the earth on high mountains are about 1.75 gram calories per square centimeter per minute (76). This value corresponds to a maximum of approximately 12,000 foot candles (75). Values at sea-level are rarely above 1.5 gram calories per square centimeter per minute, or 10,000 foot candles. These figures should be kept in mind in reading some of the earlier ecological studies of the light factor, since investigators have reported values of 17,000 to 20,000 foot candles, which obviously do not occur in nature.

The distance of the sun from the earth, which is greatest in early July and at a minimum in early January, does cause an appreciable influence on the intensity at the earth's surface. For the same solar zenith distance,⁴ the intensity is about 10 to 15 per cent. higher in the winter.

Even greater variations in the amount of light received at the earth's surface are caused by the influence of the atmosphere. Particles of dust, smoke and even gas molecules cause a scattering of light. This scattering is more pronounced with the shorter wavelengths, that is, the blue region of the spectrum. Approximately one half of the light so scattered reaches the earth as skylight. Gases in the atmosphere have definite absorption bands which also change the quality of light received. Water vapor in the air ab-

³ The solar constant is the intensity of solar radiation outside the earth's atmosphere for the sun in the zenith (directly overhead) and at its mean distance from the earth. It is equal to 1.94 gram calories per square centimeter per minute.

⁴ Solar zenith distance is the angle at the observer between lines to the sun and to the zenith.

sorbs a great deal of the long wave-lengths, particularly infrared, while ozone absorbs ultraviolet. The amount of both absorption and scattering which occurs increases with the air mass traversed, or the secant of the solar zenith distance. Absorption by the atmosphere is most important in reducing the intensity of light, while diffusion is most important in changing the energy distribution. Consequently, in winter, due to the greater diffusion caused by an increased solar zenith distance, a higher percentage of red light and a lower percentage of blue reaches the earth than in summer.

One of the most important factors causing variations in the light received is the humidity of the atmosphere and the amount of cloudy weather. Arid regions have higher hourly values and higher yearly totals than humid regions of the same latitude.

Similar variations occur between tropic and arctic regions. During the growing season the amount of light received during the average day in the tropics is not necessarily greater than the amount received in temperate regions, and only slightly greater than the amount received in the arctic regions (93). The hourly maxima are, of course, greater in the tropics than in the arctic regions. Also, the yearly totals are higher in open country than in smoky cities. An excellent summary of light-climate is given by Kimball (76) which has been freely drawn upon in the above discussion. An earlier but less comprehensive summary of light-climate is given by Rübel (132).

In the above discussion little has been said about variations in the radiation intensity during the course of a single day. The effective energy which reaches any point on the earth's surface at any instant is composed of skylight and the vertical component of direct sunlight which varies directly as the cosine of the solar zenith distance. Consequently for any station we have a continual change in both the intensity and quality of solar radiation received from hour to hour, from day to day, and from season to season.

The Effect of Light-Climate on Plants

Variations in light caused by differences in latitude, altitude and climate naturally affect rate of photosynthesis and growth of plants. Since during the growing season the difference in light between tropic and temperate regions is not very great, we might

expect that photosynthesis would proceed at approximately the same rate in both regions. Stocker (165) has found this to be the case. Plants in the tropical rain forest assimilated carbon dioxide no more rapidly than plants similarly exposed in the temperate regions. Studies by Müller (111) and by Kostytshev, Tschesnokov, and Bazyrina (89) have shown that in arctic regions plants may assimilate carbon dioxide continuously and that the total amount assimilated during the 24-hour arctic day may be almost as great as would be assimilated during a summer day in temperate regions.

Instead of being the limiting factor, light intensity in the arctic may be excessive. Lipmää (93) has pointed out that many arctic plants develop the same type of protective features against intense light that are characteristic of desert plants in temperate climates. In other words, xerophytes and mesophytes occur in the arctic regions as well as in warm regions. Arctic xerophytism is probably accentuated by the low moisture supplying power of cold soil which may be of more importance than physical dryness of the soil (29).

The exposure of tomato plants and certain others to 24-hour illumination in temperate regions, either continuous artificial light or daylight supplemented by artificial light of high intensity, results in severe injury and death (8). The injury observed is diminished if the plants receive some daylight or if the Mazda lamps are supplemented by mercury arcs. The unfavorable effects observed may be due to the unfavorable quality of artificial light, since Darrow (31) has shown that tomatoes and other plants will grow and thrive under continuous daylight of the arctic regions.

Many evergreen plants are able to perform photosynthesis in winter at a sufficiently rapid rate to more than balance the carbohydrates used up by respiration, even at temperatures near freezing (183, 73, 35). The total amount of photosynthesis which occurs in winter, however, is probably of minor importance since during the winter months profound changes occur in the arrangement and size of the chloroplasts, which are accompanied by their inactivity (122, 59, 73).

Light in Local Habitats

Plants which grow in the forest and those which grow under water are subject to light which has undergone additional modifi-

cations. The intensity of light available for plants growing under water below a depth of one meter, decreases more or less uniformly with depth (18). Water absorbs energy in the infrared and red region to a much greater extent than in the blue, hence plants in clear water receive a relatively large percentage of light within the region 440 to 580 $m\mu$ ⁵ (19, 13, 27). Particles suspended in the water cause a scattering of the blue rays more than the red; therefore, light which has passed through turbid water tends to have a lower percentage of blue than that passing through pure water (27). Consequently, both the quality and intensity of light available for submerged plants is dependent on the depth at which the plants are growing and the turbidity of the water.

A number of studies have been made on the rate of photosynthesis of submerged plants. Obviously, plants cannot live indefinitely in light intensities too low to permit sufficiently rapid photosynthesis to balance the carbohydrates used up in respiration. The depth at which the compensation point occurs naturally depends on both the species and amount of light available to the plants. Bourn (21) found that at least four per cent of radiant energy was required for the growth of *Potamogeton pectinatus*. Clarke and Oster (27) found that the point at which photosynthesis just balanced respiration for certain phytoplankton occurred from 7 to 20 meters in turbid water, and at 30 meters in clearer water. The total radiation intensity was about three per cent in each case. Schomer (137) found that the optimum depth for photosynthesis in lakes of northern Wisconsin was at the surface on cloudy days and at a depth of about five meters on fair, bright days. The compensation point was between 10 and 15 meters. In the more turbid lakes these depths were less.

For each type of water plant there seems to be a more or less optimum intensity for photosynthesis (109, 63, 78). The brown and green algae require higher light intensities for a photosynthetic balance than the red algae (175, 109). Seybold (143) has shown

⁵ Millimicrons. One millimicron = .000001 millimeter or 10 Ångstrom units. The solar spectrum may roughly be divided as follows:

Wave-lengths	290-400 $m\mu$	ultraviolet
	401-492 $m\mu$	blue
	493-535 $m\mu$	green
	536-620 $m\mu$	yellow
	621-720 $m\mu$	red
	721- $m\mu$	infrared.

that the red algae absorb a greater percentage of blue light than either the green or brown algae, which may account in part for their ability to live at greater depths.

Light in the Forest

The light available for growth of plants on the forest floor may be greatly reduced in intensity. Frequently this reduction amounts to as much as 90 to 99 per cent (11, 32, 49, 52, 132). Moreover, the intensity fluctuates almost continuously due to movements of the foliage. The intensity in sunflecks may be as high as 30 to 40 per cent of full sunlight, while in the shadow the light may be as low as two to five per cent. Where an understory of either young growth or shrubs occurs beneath a closed canopy, the light intensity is generally around 20 per cent above this second story, but may be reduced to from one to five per cent below it (70, 149).

Not only is the intensity of light in the forest lower than that in the open, but the quality is also changed due to differential absorption and reflection by leaves. Knuchel (79) found that the change in light quality under canopies of needle-leaved trees was slight but beneath broad leaved canopies the light was relatively higher in percentage of green. He studied the spectral transmission of leaves and found a much higher transmission in the green region than in the blue or red regions of the spectrum. A large number of studies on the reflection, transmission and absorption of leaves have been carried out since then which confirm these findings (11, 12, 32, 62, 119, 135, 138, 139, 140, 141, 142, 143, 154, 155, 160, 167).

Light Requirements as to Intensity

It follows from the discussion of light-climate, that light intensity during the growing season is adequate for satisfactory growth of plants in all latitudes from the tropics to the arctic regions. In fact, the intensity may be so high as to cause injury to plants, particularly to young seedlings (57, 82, 92, 174).

In desert regions where light intensities are particularly high, plants actually make use of only a small fraction of the light available. It has recently been shown that when leaves are exposed under conditions favorable for rapid photosynthesis, the rate of photosynthesis tends to decrease with increasing time, due to an accumulation of carbohydrates in the leaves (66, 90). This is spoken of as "solarization" of leaves.

A number of German and Russian workers have studied the rate of photosynthesis of plants in natural habitats, particularly of desert plants (20, 56, 83, 84, 85, 86, 87, 88, 110, 136, 156, 184). These workers have found that the daily rate of photosynthesis shows marked fluctuations. Frequently a maximum occurs around 9 to 10 o'clock in the morning and sometimes even earlier. A minimum occurs about noon when some plants may even give off carbon dioxide while a secondary maximum in the afternoon is not uncommon.

Several factors probably influence the rate of photosynthesis under desert conditions so that it does not attain as high values as would occur in the more favorable habitats. High temperature and insufficient moisture supply are probably most important while solarization of leaves is probably secondary. Miller and Burr (107) have shown that a number of plants will give off carbon dioxide in light of 2000 foot candles when exposed to temperatures of 35° to 37°C. Measurements of stomatal aperture show them to close in the light when moisture supply becomes low. Stålfelt (158) and others (50) have shown that the hourly rate of photosynthesis follows closely the size of the stomatal aperture. Hence both photosynthesis and transpiration may decrease under conditions of high light intensity and limited moisture supply (20, 26, 136).

Espino and Pantaleon (36) have found that under conditions of high light intensity, plants exposed to full sunlight in the morning and shaded in the afternoon, produce much better growth than those exposed to sun all day, or those exposed to the afternoon sun only. This is in agreement with the results on photosynthesis.

Several attempts have been made to correlate the rate of photosynthesis with measurement of external factors, including temperature, humidity, transpiration, evaporation, carbon dioxide concentration of the air and light intensity (20, 32, 58, 109, 136). Most of these have not met with particular success. Since photosynthesis is dependent on a number of external factors, first one then another may be limiting, and this appears to be the case when attempts at correlation are undertaken. During part of the day, photosynthesis may be correlated with light. Later on in the day it may be correlated with transpiration, when this

factor is closely related to stomatal aperture, and under certain conditions it has been found to be correlated with carbon dioxide concentration.

While Beljakoff (16) has found that the rate of photosynthesis should change rather gradually during the day unless other factors fluctuate violently, and questions whether the rapid fluctuations reported by Kostichev, Rosumov and Tschesnokov (87) might not have been due to inaccuracies in their methods, the work of other investigators seems to indicate that under natural conditions, light intensity, carbon dioxide supply, water supply and many other factors affecting photosynthesis, are subject to violent fluctuations and that these fluctuations cause similar variations in photosynthesis.

Although there has been considerable controversy over the exactness of Blackman's theory of limiting factors in photosynthesis, there can be no doubt of its application when broadly interpreted (67). Often two or more factors may be near limiting values (156 *a*) so that changes in these together with rapid changes in internal factors may account for the wide fluctuations in photosynthesis which have been reported.

The increase in dry weight of plants growing under natural conditions is closely associated with their rate of photosynthesis (32, 58). For best development, most plants require full sunlight, provided other factors are not limiting. With increasing light intensity, there is generally an increase in rate of growth up to 50 or 100 percent of full sunlight (146). This appears to hold true both for plants grown under carefully controlled conditions and also for plants growing in the woods (28, 32, 49, 80, 99, 131, 149). Without exposure to full sunlight for at least a part of the day, plants do not develop satisfactorily (36). Light shade is sometimes beneficial, especially if the plants are grown under conditions of suboptimal water supply, since transpiration loss tends to be directly correlated with radiation intensity (103 *a*, 10).

Plants with adequate food reserves, if kept in darkness, have exceptionally long internodes, are devoid of chlorophyll, have only rudimentary leaves and poorly developed roots (150). If plants are exposed to light of very low intensity, the leaves unfold and become green and the internodes are somewhat

shorter. As the light intensity is increased up to a value of approximately 20 to 50 percent, leaves attain a maximum size. At this point the height of the plant is also maximum. A further increase in light up to full sunlight results in plants with a slight decrease in height, in length of internode, and in area of leaves, but with an increase in percentage of dry weight, in number of branches, in size of roots, and frequently also in flowers and fruit (1, 53, 63, 64, 28, 116, 117, 131, 146, 161, 177).

The actual light intensity required for the survival of plants, if other conditions are favorable, is low—one to five percent (52, 146)—and is close to the value at which photosynthesis balances respiration (23, 72, 158, 159). However, under field conditions, it is not possible for plants to survive indefinitely with such low intensities, since they must be able to produce sufficient food reserves to enable them to meet the other unfavorable conditions which almost always prevail. Plants can be found in hardwood stands where the intensity of light is below five percent, but Daxer (32) has noticed that with many of these plants, photosynthesis exceeds respiration only in the spring before the leaves of the overstory are developed. The real shade plant then is not so much one which can grow under conditions of low light intensity, but rather one which can exist for a long period under conditions which are unfavorable for photosynthesis. When exposed only to light of low intensities, such plants probably have a much lower basal metabolism than sun plants.

Light intensity also influences, to some extent, the mineral nutrition of plants, particularly their nitrogen metabolism. Unless plants receive enough light for rapid photosynthesis, they accumulate but cannot utilize nitrogen effectively and, conversely, if they do not receive sufficient nitrogen they accumulate but cannot utilize carbohydrates effectively (68, 108, 125, 126, 127, 128, 129, 130, 160, 161, 166). Apparently light intensity affects nitrate metabolism only indirectly through its influence on carbohydrates. It has been shown that corn plants will absorb nitrogen equally well whether the nitrogen is available only during the day or only during the night, and that both series of plants will attain approximately the same total dry weight (50 a). Light influences, but to less extent, the iron, calcium and potassium metabolism of plants (60, 96).

Light Requirements as to Quality

Recent studies on the effect of different wave-lengths of light on the opening of stomata have shown that they respond about equally to light in the yellow, blue and green regions, but respond somewhat more weakly in the red. Stomata ordinarily do not open in infrared (113, 134, 156).

Even though the light in forests is changed considerably in spectral energy distribution, it still contains a sufficient percentage of the various wave lengths in order to induce approximately normal growth of plants. While the red and blue have been found by many investigators to be somewhat more efficient in photosynthesis than the green, their findings are based on intensities of incident energy rather than intensities of energy actually absorbed by the leaves. Where care has been taken to make sure that equal amounts of energy are absorbed, the green region has been found to be not only valuable for photosynthesis (25) but to lie between red and blue in its relative efficiency (45, 179). Furthermore, some 40 to 70 percent of incident green is absorbed by leaves (138, 139, 140, 142) and this certainly cannot be dismissed as valueless (142) as some investigators have seemed to think (32).

When plants are deprived of blue, but grown with full complement of red and infrared, they develop many of the characteristics of etiolated plants (44, 51, 61, 77, 118, 120, 146, 162, 163, 167). This has led several investigators to conclude that red acts on the plants like darkness, and that blue has the same effect on plants as reduced "white light."⁶ Recent studies by Johnson (74) and Arthur (6) indicate that the real factor causing the excessive elongation is infrared rather than red, and that this etiolated effect can be greatly reduced by increasing the intensity of light in the red region. Since sunlight is far richer in radiation within the visible region than the ordinary artificial lights used, plants grown even under reduced intensities of sunlight rarely show the pronounced etiolated effects characteristic of those grown with only red and infrared. Small changes in

⁶ The term "white light" is used by many investigators to designate sunlight, or even artificial light in which all wave lengths are represented. When so used it covers a multitude of variations and is in no case adapted to precise expression. In the writer's opinion its use should be discouraged and the name of the actual source designated.

the quality of light, such as occur in incandescent lamps of different wattage and efficiency, produce no noticeable effect on the growth and structure of the plant provided the total intensity as measured in foot candles is the same (7).

The actual effect of blue acting alone on the growth of plants is not well known, since it is difficult to get blue of sufficiently high intensity to produce a rapid rate of growth. While it is claimed that blue acts mainly as reduced "white lights," *i.e.*, it produces plants normal in shape but smaller in size, the writer is of the opinion that blue has a tendency to cause shortened internodes and to produce a smaller, more compact plant than would be produced under full daylight of the same intensity (146). All of the studies made seem to point toward the conclusion that full sunlight as normally received at the surface of the earth, even though it varies greatly in quality, is far more satisfactory for the growth of plants than any portion thereof, or than any artificial source which has yet been discovered (104, 105, 106, 146, 168).

While reduction in the red and blue in the spectrum which occurs in the forest may slightly reduce the efficiency of the light (168), plants do live and survive there and the intensities required are not much greater than are required when normal daylight is supplied to them, but reduced in intensity by the use of neutral screens. Certainly plants grown in the shade of forest trees have not revealed any such pronounced changes in structure as are found in those plants which have grown under definite spectral regions (32). Therefore, it may safely be concluded that the changes in spectral energy distribution of light in the forest have only a secondary influence on the growth of plants on the forest floor, and are of far less importance than the change in intensity.

Some seven or eight years ago, rather elaborate claims were made as to the importance of ultraviolet radiation for plants. Experiments seemed to indicate that ultraviolet stimulated the rate of growth, that it was necessary for the prevention of etiolation effects, that it caused an increase in the yield of glucosides in *Digitalis*, and that it had a number of other vital effects (42, 100, 101, 102, 103, 144, 145). A critical review of most of this work has shown that other factors such as increased total light

intensity, increased intensity in the blue region, increased temperature, exposure to ozone, and many other factors which accompanied exposure to ultraviolet radiation may be responsible for most of the differences noted (91, 104, 105, 106, 121). Ultraviolet does have a pronounced injurious effect on plants, especially ultraviolet of shorter wave lengths than those found in sunlight (43). With prolonged exposures to high intensities of ultraviolet at 290 $m\mu$, which is the short wave length limit of sunlight, slight injuries have been observed (9). Ultraviolet beyond that found in sunlight also renders the mechanism of photosynthesis inactive without any detectable change in chlorophyll (5).

A possible beneficial effect of ultraviolet on plants is its effect in increasing the vitamin D content (97) and also in favoring assimilation of calcium. Stewart and Arthur (164) have found that plants grown under conditions of low light intensity, if given exposures to ultraviolet, had an increased calcium and phosphorus content. No increase in these elements could be obtained in plants cultivated under full sunlight in fair weather. Similar effects of ultraviolet on calcium metabolism have been reported by Benedict (17). Ultraviolet light, or at least blue and ultraviolet, also appear to cause an increase in the assimilation of nitrate (170, 171).

The true role of ultraviolet in the region of 290–310 $m\mu$ in the growth of plants is still an open question, and while this region may have some favorable effects (182) its importance in determining the distribution of plants, as postulated by Ivanoff (71), is as yet a matter only for conjecture. Certainly, there is little justification for assigning to it the same importance as to intensity and duration of light.

Other Factors Varying with Light in the Forest

For a proper evaluation of the effect of light on the growth of plants in natural forest habitats, an understanding of the many other factors influenced by the forest is necessary. Wind velocity is reduced. Air temperature is usually reduced, but may sometimes be higher in small openings, particularly when cool winds are blowing; evaporation is decreased; and a number of other factors changed (2, 55). One factor which has until recently

received comparatively little attention, is the increased carbon dioxide concentration of the air in forests (32, 40, 98, 136). Just how valuable this factor is to the plant is not definitely known, but from measurements under laboratory conditions, it would seem that it may have a very important effect, especially when other conditions are also favorable for photosynthesis. Whether the roots of plants can actually absorb carbon dioxide from the soil which may be used in the leaves, is still open to question (95). In order for the carbon dioxide of the soil to be injurious to the roots of plants, it would have to reach a concentration of two percent by volume of soil atmosphere (40).

The factor which has received by far the greatest amount of attention besides light, is that of root competition. This was first called to attention by Fricke in 1904 (41) and has been emphasized particularly by Toumey (172) in this country. The roots of forest trees draw heavily upon the soil for both moisture and nutrients. When the roots of older trees are excluded from a small plat of ground by trenching around it, the plants within this plat usually show an important increase in their rate of growth and many new individuals may become established (15, 37, 38, 39, 30, 81, 173). This has led some individuals to ascribe to root competition the dominant role in determining the composition and growth of the understory (172). However, it has been pointed out that the root competition which tree seedlings must withstand is often just as great or greater in grassland (114, 115) and that during periods of severe drought, the ameliorating effects of the shade provided by the overstory enables plants to survive better in the forest than in the open (151). Studies of Fabricius (37, 38, 39) and others (30, 148) indicate that both light intensity and root competition are important factors in the growth of plants under forest canopies, and that improved growth can be brought about either by an increase in light intensity or by the elimination of root competition, or by both. Neither factor can safely be neglected.

Plants grown under light conditions which favor the accumulation of carbohydrate reserves are much more able to resist drought and frost, provided exposure conditions are the same, than plants grown with a minimum supply of light (33, 34, 152, 176).

Just what ecological effect length of day may have on the growth of plants under natural conditions, aside from its influence on flowering and fruiting, is not well known. It has been shown that only very low intensities of light supplementary to daylight are required to bring forth the photoperiodic response in plants (123, 124, 181). Undoubtedly, length of day through its influence on flowering, fruiting and dormancy, does have an important effect on the distribution of plants (46, 47, 48), but whether important effects on mineral nutrition are caused by length of day under natural conditions, is problematical.

Light and Succession

Ecologists have ascribed to light a dominant role in plant succession. It is commonly assumed that the chief reason why a given species of forest tree fails to succeed itself is due to the inability of its seedlings to grow in the shade of the parent trees, whereas seedlings of the succeeding species are able to do so. From observations on plants grown under different light conditions both in artificial shades and in the forest, the writer has come to the conclusion that this conception is not entirely in accord with the facts and the following explanation is offered as being more probable.

When light intensity is too low for the growth (increase in dry weight) of species intolerant of shade, it is also too low for appreciable growth of the most tolerant. The real difference between the tolerant and intolerant species, in so far as light requirements are concerned, is the length of time they can survive in light intensities too low for growth. When light intensities are high enough for appreciable growth of either species, the one having the most rapid rate of growth, which is usually the least tolerant, will outgrow the other.

There is considerable difference in requirements of different species for germination and establishment of their seedlings. Seedlings of tolerant species are generally better able to become established on the forest floor; in fact, shade appears essential in some species (153). Once established they can exist for a long time without making appreciable growth, whereas the intolerant seedlings, if established, soon die out. This results in an understory made up almost entirely of tolerant species. When

favorable light conditions occur, due to the death or removal of a large tree in the overstory, the tolerant seedlings increase in growth and appropriate the openings before intolerant ones seed in.

Studies of plant distribution and growth in relation to light intensity have been made by a number of investigators whose findings are in accord with the explanation of succession given (3, 12, 65, 133, 148).

Light Measurement⁷

Light may be measured by measuring its chemical, illuminating, electrical and heating effects. All instruments based on the first three effects are selective in nature, that is, they are unequally sensitive to different wave lengths. Only methods which depend upon the heating effect of light are uniformly sensitive throughout the spectrum.

There has recently been a tendency on the part of plant workers to abandon instruments based on chemical and illuminating effects in favor of instruments based on electrical effects of light. Several photoelectric cells are available which may be satisfactorily employed for measuring light in the field. Recently a new cell has been introduced in Germany and in this country which does not require an external source of electrical potential for its operation. These cells are very convenient and are sufficiently rugged for field use. They are being adopted by a number of plant workers (7, 142, 178). These cells seem to be subject to many of the same shortcomings of conventional photoelectric cells. If exposed to the intensity of full sunlight, they are subject to solarization, which results in a decrease in the current produced with increasing exposure time (6), and they are, of course, selective in their sensitivity. The sensitivity curve of these cells is very close to that of the human eye, and for this reason their use is favored by a number of plant workers. However, it should be borne in mind that there is no evidence to indicate that the plant responds to the different wave lengths of light in the same degree to which the human eye does, even though photosynthesis is confined mainly to the visible region.

⁷ A rather complete survey of methods of measuring light was published in 1931 (147) which deals with the advantages and limitations of the various types of instruments. Discussion here will be limited mainly to instruments and methods which have appeared since then, together with a discussion of the technique of taking measurements in the field.

A number of workers have been unwilling to use non-selective radiometers for measuring the light available to plants because of their sensitivity to infrared, which was supposed to exert only a heating effect on plants. However, with the recent discovery of the influence of infrared in producing elongation, this portion of the spectrum can no longer be neglected. The writer is of the opinion that non-selective radiometers may safely be used for measuring the intensities of solar radiation available for plants, and also for measuring artificial radiation, provided the spectral energy distribution is known. For measuring radiation in the visible region only, thermopiles and other non-selective radiometers may be equipped with either glass or solution filters which absorb infrared. Photoelectric cells, because of their high sensitivity, are more satisfactory for measuring narrow spectral bands when the energy output is low. Discussion of some of the newer photoelectric cells are given by Atkins and Poole (13, 14), Neurnbergk (112), Volk (178), Thomson (169) and Howlett (69).

Arcichovsky (4) has developed a new method of recording the intensity of sunlight by exposing photographic paper. New thermopiles have been developed by Withrow (180) and Brackett (22). Hall (54) described the use of thermometers having blackened and whitened bulbs, which may be used for rough approximations. Almost any instrument gives better results than a guess, since the human eye has such a wide range of adaptability to light that it is almost impossible to estimate light intensity accurately, even by practiced observers.

There has been some contention among ecologists as to whether light should be measured by using a plane or spherical absorbing surface, and if a plane surface is used should it be oriented normal to the sun's rays or exposed in a horizontal plane (94, 24, 49). It is argued that an individual plant does not have all its leaves in a horizontal plane, hence a spherical surface is preferable. This argument is sound when the investigator is concerned only with individual plants, but when the growth of vegetation on a given area is considered, then only the horizontal component of sunlight is available. Since weather observers usually base their measurements on the energy absorbed on a horizontal surface (76) it is desirable for plant workers to follow their lead, especially when comparing light conditions and growth in two widely separated regions.

Another point which merits consideration is the accuracy of measurements in the forest. Gast (49) has recommended a minimum of 40 complete daily records, well distributed throughout the growing season, to get a significant average of the radiation available beneath a canopy. Even then the value applies only to the particular point where the instrument is located. The writer has found that 20 to 40 direct readings made at uniform intervals over the area of a 1/10 acre plot will give an average accurate to within five percent if the canopy is not too uneven. Two averages determined in this manner on the same plot, but at different times of year, usually agree to within five to ten percent, especially if the measurements are taken with the sun at approximately the same solar zenith distance.

Most ecologists will be obliged to work with direct reading rather than recording instruments and each will have to determine for himself how many separate readings are required to obtain the desired degree of accuracy.

The development of instruments and technique for measuring light suitable for ecological use has advanced rapidly during the past ten years and as more and more ecologists adopt the newer methods, we may expect an increase of important discoveries in the field of light and its influence on vegetation.

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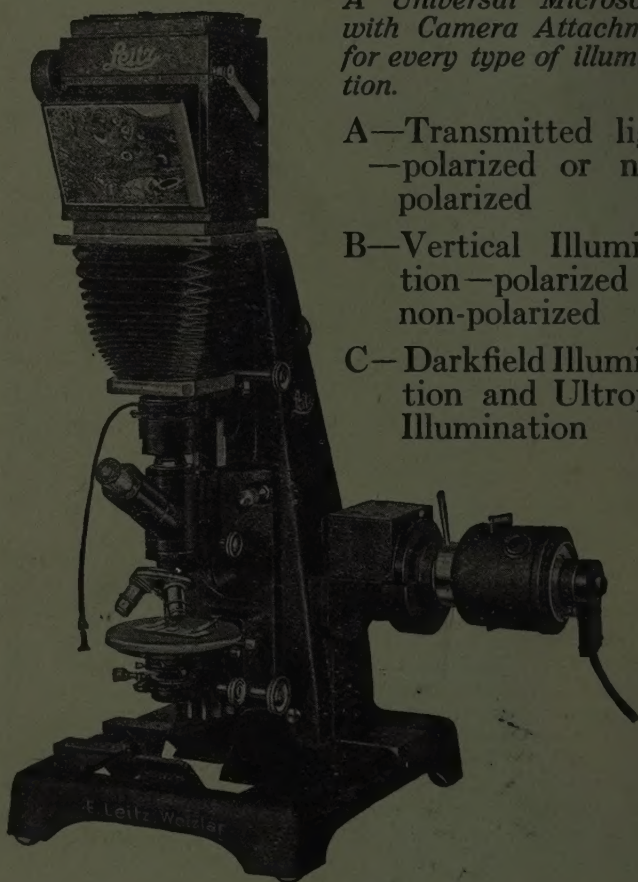
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